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EVAPORATION AND SOIL MOISTURE IN RELATION TO THE SUCCESSION OF PLANT ASSOCIATIONS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 191

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(WITH TWENTY-SEVEN FIGURES)

I. Evaporation

The water conditions of plants have long been recognized by ecologists to be matters of the highest importance, but unfortunately it has seldom been possible to describe these conditions in other than the most general qualitative terms. The only factor affording quantitative data has been precipitation, and this is only indirectly related to plant production on account of the many irregular variations that exist between the amount of rainfall and the quantity of water available for plant growth. In a general way, and especially in dealing with large areas, a fairly close relationship may be established, but within the different habitats of a single region no such connection can be recognized.

In a study of water conditions, two phases of the subject are of importance. They are the direct source and amount of the supply and the region and cause of the loss. The latter is a climatic, the former largely an edaphic, problem, for it is evident that plants derive their moisture from the soil and lose it into the air, and for the quantitative solution of these problems it is necessary to measure the power of the air to extract water from the plant; in other

words, the evaporating power of the air, and the amount of moisture in the soil available for the use of plants. Such measurements have been carried on in certain parts in the Chicago region in an effort to establish a relation between the moisture conditions and the succession of plant associations.

The researches of LIVINGSTON (1) and others have shown that the evaporating power of the air is a rather satisfactory summation of all the atmospheric factors that determine and limit the growth of plants, since it indicates the power of the atmosphere to extract water from their aerial parts, and has been shown in general to vary almost directly with their rate of transpiration. He has also devised the porous cup atmometer and shown that it is able to measure this power with a very considerable degree of accuracy during the growing season, or rather during that portion of the year free from frost, which in the Chicago region is practically the same as the growing season. Hence, during the three seasons of 1910–1912 stations with these atmometers were established and maintained in six distinct plant associations in the Chicago region. Since nowhere in this region is a succession of associations more clearly marked or more easily determined than upon the sand dunes immediately south of Lake Michigan, it seemed that a large number of the determinations should be made within this area. This vegetation has been described by COWLES (2), who has shown that the forest succession consists principally of associations dominated by cottonwood, pine, black oak, white and red oak, and beech and maple, in the order named. These represent a continuous series extending from pioneer trees to the mesophytic climax forest of the region. The physiographic factors, the detailed composition of the associations, the variety of the transitional forms, and the frequency of retrogression have been so well explained by COWLES that further detailed discussion at present seems unnecessary. While all the associations mentioned occur upon the sand dunes in the order indicated, it was found to be impossible to obtain easy access to the two final stages of the succession upon sand, and hence the oak-hickory and beech-maple forests were upon clay soil. Objections may be urged against such a selection, and many are recognized by the writer, but it is maintained that the comparisons

that have been made in this investigation are quite legitimate ones, and, further, it is hoped that future studies may supply the lacking data for these associations upon a sandy soil. In addition to this successional series of associations, through the cooperation of some of the writer's students, data were obtained from the edaphic prairie characteristic of the Chicago region.

The period of investigation was during 1910, from May 6 to October 31 (178 days); during 1911, from May 1 to October 28 (180 days); and during 1912, from May 3 to October 22 (172 days), the records for the oak-hickory forest and the edaphic prairie being for the seasons of 1911 and 1912 only. Weekly visits were made to all stations throughout this period, except to those of the beech-maple forest, which were visited once in two weeks. A preliminary report of much of the data obtained during the first season has already appeared.[1]

INSTRUMENTS AND METHODS

The instruments employed were mostly the porous cup atmometer devised by LIVINGSTON, although during the first season a few of the type described by TRANSEAU (3) were also used. The atmometers were mounted in wide-mouthed bottles, having a capacity of 500 cc., closed with tightly fitting cork stoppers that were perforated for the atmometer tubes and for bent capillary glass tubes which served to equalize the atmospheric pressure within the bottles with that of the exterior air, without causing any loss by evaporation or permitting rainwater to enter the reservoir. The bottles were sunk in the soil about two-thirds of their height, so that the evaporating surface of the instruments was 25–20 cm. above the surface of the soil. Except where otherwise specified, the readings were made weekly by filling the bottles from a graduated burette to a file scratch on the neck. The small area of the water surface at this point made the probable error in readings less than 0.5 cc., and this could have had no appreciable effect upon the results. The instruments were all standardized to the same unit before being used, restandardized at intervals of 6–8 weeks during the season, a revolving table being used for the purpose similar to

[1] BOT. GAZ. **52**:193–208. 1911.

that described by NICHOLS (4), and a final correction made on their being collected in the autumn. By the coefficients thus obtained, all readings were reduced to the standard adopted by LIVINGSTON (5), the directions he gives being so closely followed that it is unnecessary to detail further the methods used in operating the instruments. Three or more stations were always maintained in each association, the mean of the various readings being taken as giving the true measure of the evaporating power of the air for that association.

In most instances no correction has been made for errors caused by rainfall, although during showers some water undoubtedly passes into the porous cup and into the reservoir, because it was thought that the amount of variation thus produced would be the same for all stations within so limited an area, and hence the comparative relation of results would remain unchanged. This assumption has been largely verified by BROWN (6), using an atmometer with a rain-correcting valve, and also by the experience of the writer by maintaining control instruments with the valves. The record for the prairie association for 1911 was wholly, and that for the oak-hickory forest for 1912 was partially, made with rain-correcting atmometers.

In order to facilitate comparisons between the various stations, and to exhibit the progress of the evaporation rate during the entire season, the average water-loss per day between the weekly readings has been calculated, and the results expressed in graphs, with ordinates representing the number of cubic centimeters lost per day by a standard atmometer, the abscissas being the intervals between the weekly readings. The readings included within each calendar month are indicated at the top of the diagram. For convenience of reference, the stations are numbered consecutively, beginning with those of the association of lowest rank, that is with those of the cottonwood dune.

PLANT ASSOCIATIONS AND STATIONS

The stations established in the plant associations upon the sand dunes were all upon an area of dunes lying between the little village of Miller, Indiana, and the southern shore of Lake Michigan. The shore at this point is gradually encroaching upon the lake

because of the material being deposited off shore. This being swept inward by the waves and wind forms increasing areas of dunes, at first quite bare, but with forests soon advancing upon them. Grasses and shrubs constitute the first vegetation, but in the moist depressions the seeds of the cottonwood (*Populus deltoides*) germinate, and some of the seedlings are able to maintain themselves. A more detailed account of their establishment has been given elsewhere by the writer (7), and it is sufficient here to note that they surmount the moving dunes and at a distance of 100–200 meters from the shore establish the pioneer tree association that may be designated the cottonwood dune association, or more briefly the "cottonwood dune." This persists upon more or less actively moving sand, forming dunes varying in size up to 20 or even 30 meters or more in height, until from various causes, among which the vegetation is the most important, movement is checked and the dunes become fixed. It is an association of a single tree species and a paucity of shrubs and herbs, all having strongly xerophytic structures. Among the prominent species are *Salix glaucophylla*, *S. syrticola*, *Prunus pumila*, *Cornus stolonifera*, *Calamovilfa longifolia*, *Ammophila arenaria*, and a very few annual and perennial herbaceous plants.

In this association, upon dunes that had become almost completely fixed (fig. 1), four stations were established, each with at least one atmometer. These stations were about 200 meters from the lake shore, some 100 meters apart, and about 12 meters above the level of the waters of Lake Michigan. Three of these stations were upon comparatively level areas, surrounded by the usual open stand of cottonwoods and willows (fig. 2). At all stations the atmometers received a small amount of shade for a few hours of the day, and on account of the open nature of the association were little sheltered from the wind, the cups receiving a rather sharp sand blast during high winds. The differences of exposure to winds probably caused some of the variations in the records of the different stations, but affected very slightly the average rate for the season. Station 4 was upon the leeward slope of a very slowly advancing dune, and was further sheltered by a good stand of *Cornus stolonifera*. It was about 3 meters below the crest of

the dune upon an eastern exposure. This station was maintained only during the season of 1910. A detailed report of the atmometer readings for the four stations during the season of 1910 is shown in fig. 3, where in addition to the evaporation records the weekly rainfall in centimeters at Chicago during the summer months is plotted. As it has been possible to establish no direct relationship between rate evaporation and the occurrence and amount of precipitation, rainfall data are omitted from the remaining diagrams.

FIG. 1.—Sand dunes with *Populus deltoides* or the cottonwood dune association still moving slowly over an area with *Pinus Banksiana*, *P. Strobus*, etc.; Miller, Ind.

An examination of these graphs will at once show that the rate of evaporation was high and subject to sudden and considerable changes. There was no great divergence in the rate at stations 1, 2, and 3, but the rate at station 4 was decidedly lower, showing the modifying influence of the shrub cover in creating less extreme conditions, which permit the entrance and establishment of species of less xerophytic nature, which eventually form the succeeding association. Thus not only does the nature of the vegetation control to a great extent the evaporation beneath it, as pointed out

by GLEASON (8) and others, but the evaporation thus controlled and changed is one of the principal factors in causing the development of a different vegetation, or, in other words, the decreased rate of evaporation caused by the heavier vegetation is the direct cause of succession between different associations. It seems surprising that GLEASON has reached an opposite conclusion from somewhat similar data.

An average of the records of stations 1, 2, and 3 is plotted for comparison with similar records from the other associations (fig. 4).

FIG. 2.—Dune with *Populus deltoides* and *Salix syrticola;* station 3; Miller, Ind.

Here it will be seen that the maximum average evaporation for any week of 1910 was just above 32 cc. per day, and the minimum only once fell below 12 cc. per day. The average for the entire season of 178 days was 21.1 cc. per day. In 1911 several days in May, with a temperature above 90° F., caused a remarkable maximum of 47 cc. per day in that month (fig. 5), and serves to emphasize the importance of records extending through several seasons. The midsummer maximum was 42 cc. per day, the minimum 11.5 cc., and the average 24.6 cc. per day. The season of 1912, on the

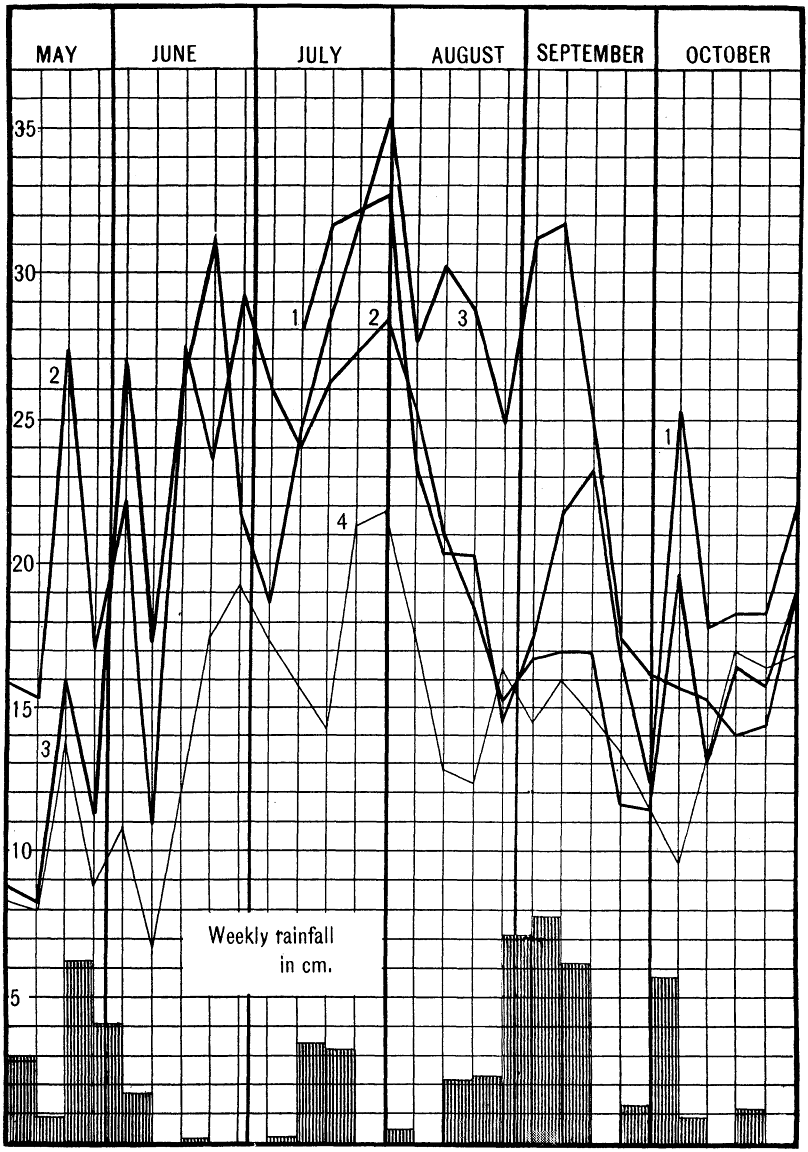

FIG. 3.—Daily evaporation rates in the cottonwood dune association at stations 1, 2, 3, and 4, during the season 1910.

contrary, was one of less extremes (fig. 6), giving a maximum evaporation rate of only 31 cc. per day and a minimum of 12.2 cc., while

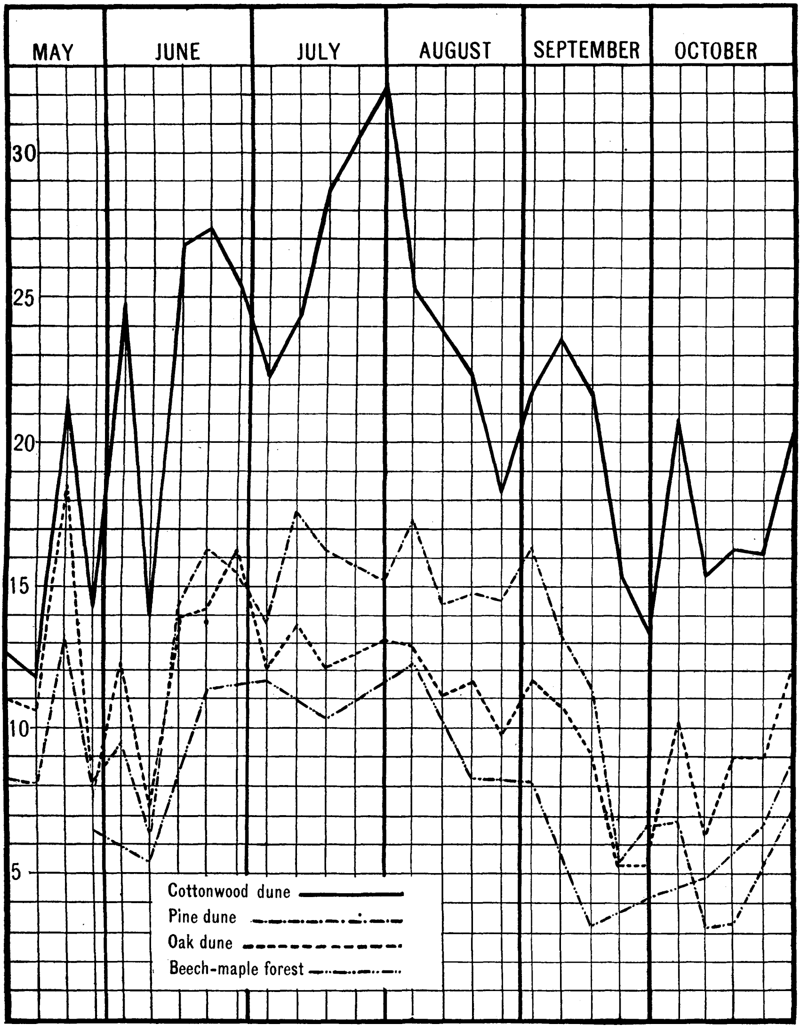

FIG. 4.—Mean daily evaporation rates in the different associations during the season 1910.

the average was almost identical with that of the first year, amounting to 21.3 cc. per day. Here the general results of the three

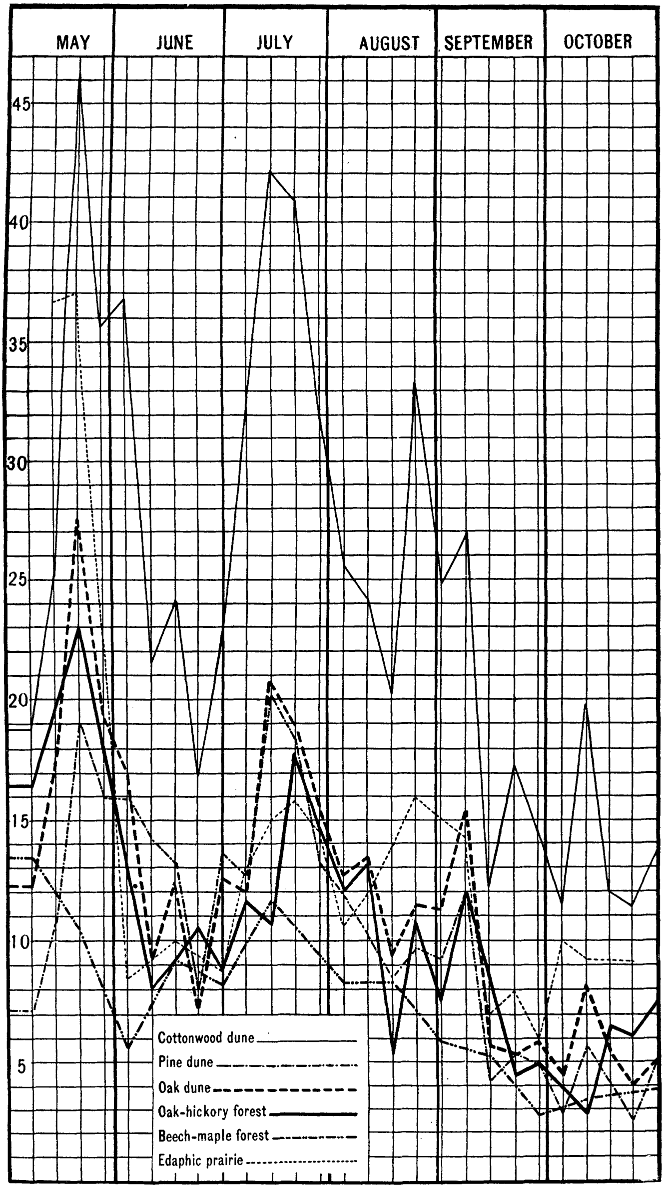

FIG. 5.—Mean daily evaporation rates in the different associations during the season 1911.

seasons investigated are seen to be consistent, and to indicate that not only is the cottonwood dune an association with a very high

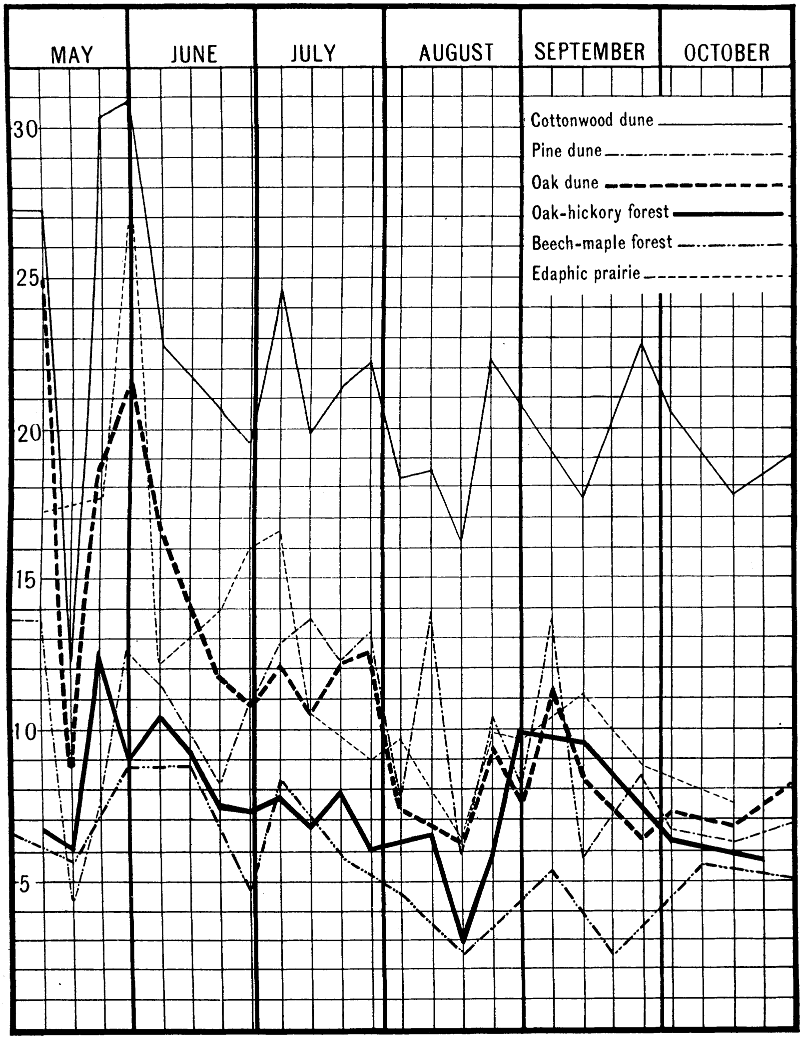

FIG. 6.—Mean daily evaporation rates in the different associations during the season 1912.

rate of evaporation, but also that it is subject to excessive variation. This is very noticeable during May and June, and prevails to a less

extent during the remainder of the season, the fluctuations being markedly greater than in the other associations.

With the fixation of dunes and the increase of grasses and other herbaceous vegetation, seedlings of conifers develop and give rise to an evergreen forest association succeeding the cottonwood, and here designated the pine dune association (fig. 7). This association varies somewhat in composition in different localities, but in the area under consideration is dominated by *Pinus Banksiana*,

FIG. 7.—Dune with *Pinus Banksiana*, *P. Strobus*, *Juniperus communis*, etc.; station 6; Miller, Ind.

associated with *Juniperus virginiana*, *J. communis*, and in older portions with *Pinus Strobus*. In the undergrowth *Arctostaphylos Uva-ursi* is conspicuous, associated with *Rhus canadensis*, *R. toxicodendron*, *Prunus virginiana*, *Celastrus scandens*, seedlings of *Quercus velutina*, *Smilacina stellata*, *Asclepias tuberosa*, *Monarda punctata*, and other woody and herbaceous plants. It is evident that this association is unique in the dominance of evergreens, while its limited extent shows that it is comparatively short-lived, a

fact that is emphasized by the presence, very early in its history, of seedlings of *Quercus velutina*, the dominant tree of the succeeding association.

In this association, stations 5, 6, and 7 were placed at spots of medium density of growth, about 100 meters south and east of the cottonwood dune series. The averages of the readings from the three stations are plotted for comparison with similar data from the other associations (figs. 4, 5, 6). Compared with that of the preceding association, the rate of evaporation is seen to be much lower and subject to less violent fluctuations. The maxima and minima are nearly synchronous with the preceding and succeeding associations, the most remarkable feature being the very low comparative rate during the weeks of May and October, when the deciduous associations are largely without foliage. The maximum for 1910 (fig. 4) was 17.5 cc. per day, the minimum fell below 4 cc., and the average rate for the season was 11.3 cc. daily.

The next season the maximum rate was 20.2 cc. per day (fig. 5), the minimum 2.5 cc. per day, and the average 10.3 cc.; while in 1912 (fig. 6) the maximum was only 13.7 cc. per day, the minimum rose to 4 cc. per day, but the average was reduced to 9.7 cc. per day, again demonstrating the fact that 1912 was a season of moderate climatic conditions.

Proceeding inland from the lake shore, the pines gradually decrease in number, and the black oak (*Quercus velutina*) becomes more plentiful, until at a distance of about 500 meters south of the last group of stations it forms an almost pure stand, with only occasional trees of white oak (*Quercus alba*). The shrubby under-growth consists principally of *Prunus virginiana*, *Rosa blanda*, *Viburnum acerifolium*, *Vaccinium pennsylvanicum*, *Ceanothus americanus*, and seedlings of *Quercus velutina* and *Q. alba*. Among the herbaceous members of the association are *Smilacina stellata*, *Lupinus perennis*, *Tephrosia virginiana*, *Lithospermum canescens*, *Asclepias tuberosa*, *Helianthemum canadense*, *Polygonella articulata*, and *Aster linariifolius*. In this oak dune association four stations were placed: nos. 8, 9, and 10 in the stands of average density (fig. 8), and no. 11 in one of the very characteristic openings sparsely covered by xerophytic grasses, together with such plants

as *Monarda punctata*, *Asclepias tuberosa*, and *Opuntia Rafinesquii.* This last station was maintained only during the seasons of 1910–1911, and, owing to a series of accidents, its record was by no means continuous, especially during the latter season. During 1910 (fig. 9) its rate of evaporation was decidedly in excess of that of the other stations, especially in June and July. The records of the other stations are quite comparable and their average appears in fig. 4.

FIG. 8.—Dune covered with open forest of *Quercus velutina;* station 10; Miller, Ind.

In 1910 (fig. 4) a maximum of nearly 19 cc. per day occurred in May, before the trees were in full foliage, and similar high rates at the same season of the year were seen in 1911 (fig. 5), when it rose to the surprising height of 27.5 cc. per day; while in 1912 (fig. 6) it was 21.5 cc. per day. This could hardly be a critical period for vegetation, on account of the abundant supply of water in the soil (see second part of this paper), although it might be decisive for many young seedlings, and it may therefore be disregarded in the general discussion.

Midsummer afforded maxima of 16 cc. in 1910, 18.9 cc. in 1911, and 12.5 cc. in 1912, the minima for these years being respectively

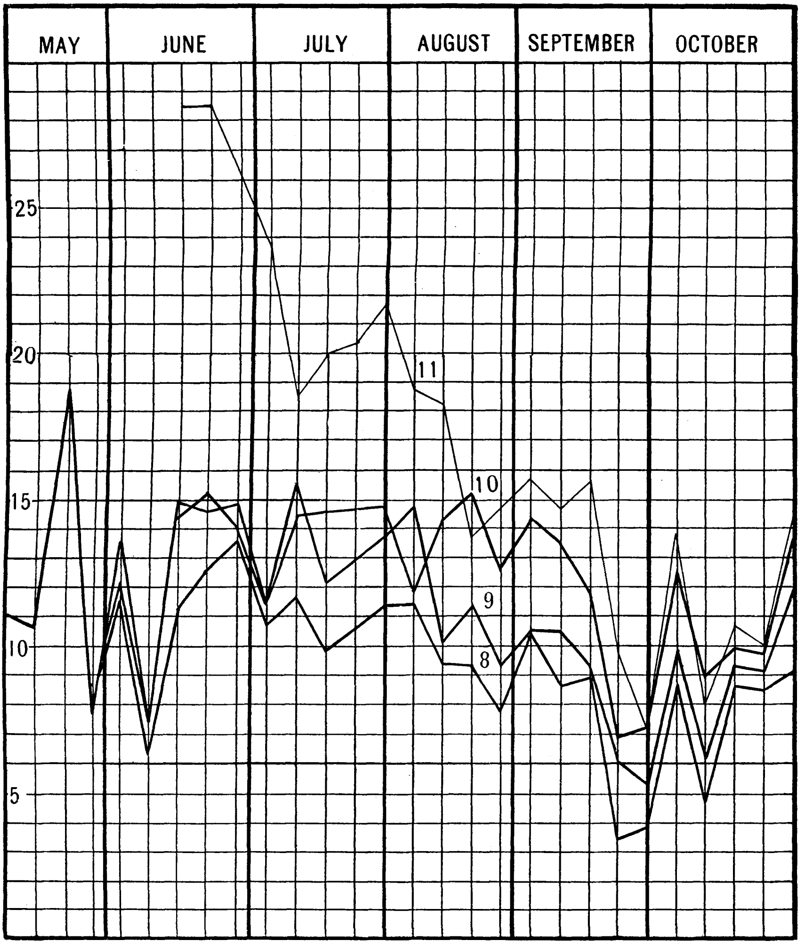

FIG. 9.—Daily evaporation rates in the oak dune association; stations 8, 9, 10, and 11 during the season 1910.

5 cc., 4 cc., and 6.3 cc. per day, while the averages for the seasons were 10.3 cc., 11.8 cc., 10.9 cc. daily (figs. 4, 5, 6).

The forest association dominated by *Quercus velutina* is rather persistent upon the dunes, but is gradually changed by the invasion

of other more mesophytic trees, notably the red and white oaks (*Q. rubra* and *Q. alba*) and one or two species of *Carya*, eventually giving rise to a fairly mesophytic association, commonly designated the oak-hickory forest. Although rather abundant in the Chicago region, it does not seem desirable to enter here upon any discussion of its occurrence or composition, especially as it has been excellently described by COWLES (**9**). Similar reasons are sufficient for very brief descriptions of the other associations included within the scope of this paper.

The most accessible, comparatively undisturbed area of this association near the city of Chicago is found about 15 miles southwest of Miller, Indiana, at Palos Park, Illinois, where it has developed upon morainic clay. Here stations 12, 13, and 14 were established in 1911 by one of my students, Mr. WADE MCNUTT, in the typical upland mesophytic forest, and station 15 in a depression which was really the floor of a broad shallow ravine and comparable in most respects to a floodplain. In the depression there were, in addition to the trees of the upland, such typically floodplain species as the white ash (*Fraxinus americana*), the elm (*Ulmus americana*), and the black walnut (*Juglans nigra*). A more detailed description of the forest and an analysis of the results of 1911 have already appeared (**10**). In this year there was an average midsummer maximum rate of 17.5 cc. per day (fig. 5) from stations 12, 13, and 14; a minimum rate of 2.7 cc.; and an average for the season of 180 days of 9.8 cc. per day. In 1912 the midsummer maximum was 10 cc. daily (fig. 6), the minimum the same as the preceding year, while the average was reduced to 7.8 cc. daily. Comparing this rate with that exhibited by the mesophytic floodplain forest of the depression, we find that the latter had a maximum of 16.2 cc. daily in 1911, a minimum of 1.7 cc., and an average of 8.3 cc. daily (**10**). In 1912 the maximum was reduced to 8 cc. daily, the minimum to 1.5 cc., and the average rate was only 4.2 cc. daily (fig. 10).

The climax of mesophytic conditions in the northern United States appears to be a forest in which the beech (*Fagus grandifolia*) and the maple (*Acer saccharum*) are conspicuous members. The succession upon the sand dunes is found to attain this climax, a

good instance being seen at Sawyer, Michigan, but unfortunately for the purposes of our investigation no such area was available nearer Chicago, and hence recourse was had to a good tract of beech-maple forest at Otis, Indiana, about 20 miles east of the stations at Miller. In this forest, in addition to the two dominant trees, there were a few individuals of *Tilia americana*, *Prunus serotina*, and *Liriodendron Tulipifera*, while notable in the undergrowth were seedlings of the principal trees, together with *Asimina*

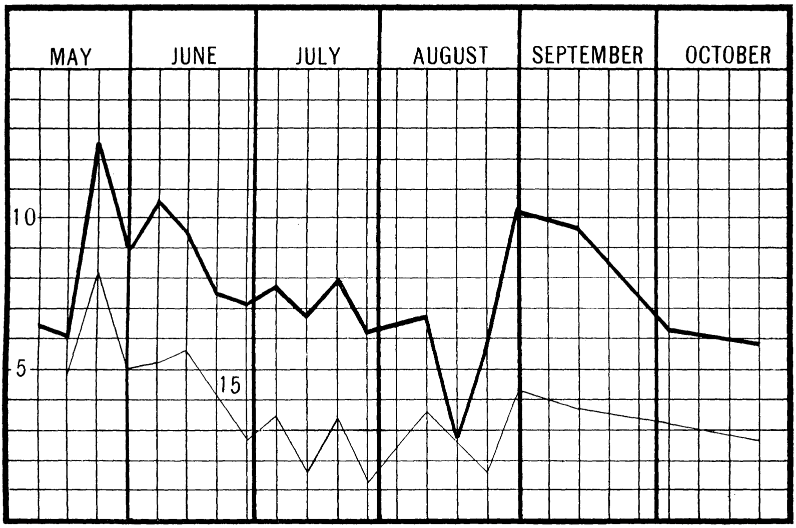

FIG. 10.—Daily evaporation rates in the oak-hickory forest for the season 1912; heavy line representing the mean rate for stations 12, 13, and 14, and light line that for station 15.

triloba, *Sambucus racemosa*, *Evonymus americanus*, and such herbaceous species as *Dicentra canadensis*, *Trillium grandiflorum*, *Adiantum pedatum*, *Polystichum acrostichoides*, *Viola rostrata*, and *Erigenia bulbosa*.

In this beech-maple forest, stations 16 (fig. 11), 17, and 18 were placed about 100 meters apart, upon the floor of the forest, station 19 in a rather narrow ravine (fig. 12) about 4 meters below the level of the others, while at station 20 the atmometer was attached to the branch of a tree 2 meters above the surface of the soil. The

last station yielded a very broken record during 1910; its record during 1911 has already been published (11), and at the end of that year it was discontinued, as other studies upon the evaporation rates in different strata were planned and in progress.

A comparison of the records of the five stations during 1911 will be found interesting and instructive (fig. 13). Stations 16, 17, and 18, upon the floor of the forest, show graphs of considerable regularity, differing but little from each other. Their combined average for the season was 7.4 cc. daily, and if this be compared with the

FIG. 11.—Beech-maple forest; station 16; Otis, Ind.

average rate from station 20, of 13.5 cc. daily, and from station 19, of 5.9 cc. daily, the proportional evaporating power of the air in the three strata will be found to be very nearly 1.84:100:0.80.

The average rates from the three stations upon the floor of the forest for the three seasons (figs. 4, 5, 6) gave maxima of 12.2 cc., 11.6 cc., and 8.1 cc. daily; minima of 3 cc., 2.8 cc., and 3.5 cc. daily; and seasonal averages of 8.1 cc., 7.4 cc., and 5.6 cc. per day respectively for the years 1910–1912.

It is interesting here to note the close correspondence between the records for this beech-maple forest and those obtained by

TRANSEAU (12) in a mesophytic forest containing a small percentage of beech, and situated on Long Island, New York, where for the period of observation from June 5 to July 2, 1907, the evaporation rate averaged 8.5 cm. daily, compared with 8.4 cm. daily during the month of June 1910, in the Otis, Indiana, forest, and 8 cc daily as the mean average rate for the midsummer weeks of the years 1910–1912 (table II). While it is not safe to draw any very definite conclusions from records covering but a single month, it

FIG. 12.—Ravine in beech-maple forest; station 19 about two-thirds down the right hand slope; Otis, Ind.

may be assumed that the two associations differ very little in the amount of mesophytism developed. It is to be regretted that similar comparisons cannot be made between the writer's results and those of GLEASON (8), but unfortunately the latter were not made with standard atmometers.

The edaphic prairie is a characteristic plant association of the Chicago region, and while it does not lie in the successional series with which this investigation is most particularly concerned, it was thought that it would be profitable to compare it with the various

forest associations. It seemed all the more urgent that it should be investigated because, with the growth of the city and the advance of agriculture, it is rapidly disappearing. Consequently, in 1911 the attention of Mr. E. M. HARVEY was directed to this portion of the problem and the range of evaporation and of soil moisture as determined, and the results have been published (13), but

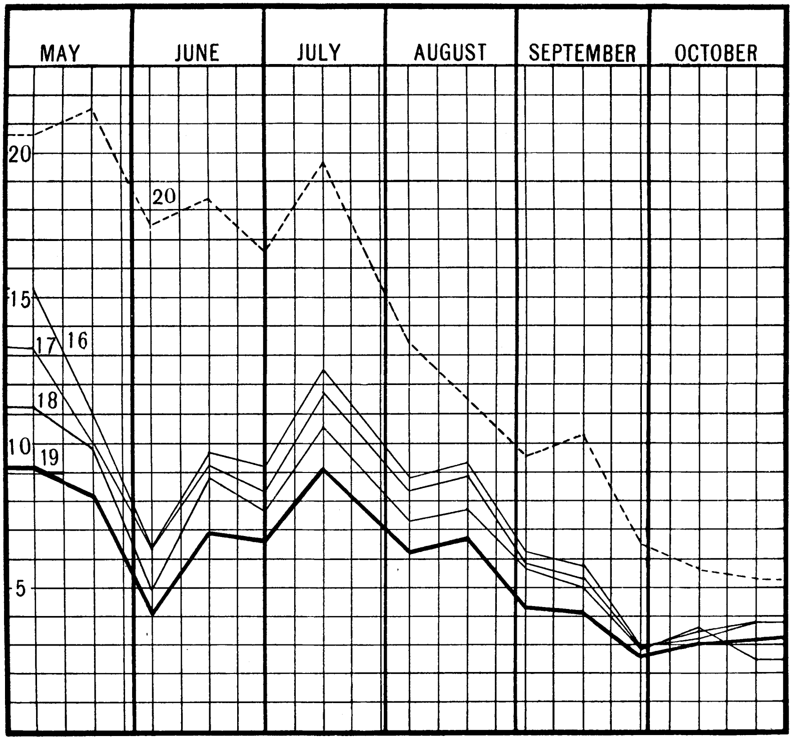

FIG. 13.—Daily evaporation rates in the beech-maple forest at stations 16, 17, 18, 19, and 20 during the season 1911.

through the courtesy of HARVEY, the averages for the year are included in fig. 5. The floristic composition of the prairie vegetation has been discussed by COWLES (9) and by HARVEY, and needs no further reference at present. This association seems to be the most usual stage in succession following the sedges in the filling up of shallow ponds and lakes formerly abundant in the Chicago region.

For the season of 1912 the prairie stations were under the efficient charge of Miss L. NEWLON, to whom the writer is indebted for the results here presented. During both seasons the range of the evaporation rate was great (figs. 5, 6), the vernal maxima being 37 cc. and 27 cc. daily, the midsummer maxima 16 cc. and 16.5 cc. daily; the minima 5.9 cc. and 6.1 cc.; while the average for each of the two seasons was 12.5 cc. per day.

GENERAL CONCLUSIONS

Several methods may be employed for comparing the data from the various associations. Perhaps the best is by means of the charts upon which the daily average rate by weeks for all the associations are plotted together (figs. 4, 5, 6). Here the characteristics of the different rates are represented graphically, and may be seen at a glance. Throughout the entire series the maxima and minima are generally coincident in time and proportionate in amount. Minor irregularities appear that it would be useless to attempt to explain. The different years show characteristically different curves. Thus, 1910 comes nearest to the commonly accepted ideas, with a somewhat regular curve increasing rather regularly from the beginning of the growing season, reaching a marked maximum about midsummer, and falling rather sharply with the humid weather of late August and September. The following year there are excessively high rates of evaporation in May (fig. 5), which will be found to correspond to a period of unusual weather conditions. The month had the highest temperature record for May experienced since the establishment of the Chicago Weather Bureau in 1871. The average temperature was 10° above normal, and for six days it reached or exceeded 90° F. The percentage of sunshine (79 per cent) was also greater than observed during any previous May. Moderate temperature conditions at midsummer, and a relative humidity slightly above the average, together with the percentage of sunshine below the normal mean are reflected in the general course of the evaporation graphs. The year 1912 is marked by a very moderate summer, the wind record of the weather bureau showing comparatively light air movement, while throughout July, August, and September the temperature

and sunshine records were considerably below the average. These weather conditions have resulted in very moderate and equable evaporation rates throughout all the associations and particularly in the more mesophytic (fig. 6). A further study of these diagrams in comparison with the data of the Chicago Weather Bureau would prove even more conclusively the assertion that the evaporating of the air represents a rather accurate summation of all the atmospheric factors that may be related to the water content of the aerial parts of plants. The differences in the records for the various years also prove the necessity of continued observation and extended records before definite conclusions are reached.

The records of 1911 and 1912 serve to give greater emphasis to some of the facts recorded and to the tentative conclusions arrived at during 1910 and published in the preliminary report[2] of these investigations. Thus, the evaporation rate of the cottonwood dune is farthest removed from the other associations, and by it there is exhibited not only a very great evaporating power, but also excessive and rapid variation, an increase or decrease of 50–100 per cent between the rates for consecutive weeks being not uncommon. This cannot but denote extremely rigorous conditions for the development of seedlings of ordinary herbaceous plants. The high midsummer maximum, apart from the question of soil moisture, would likewise prove an efficient factor in excluding all mesophytic plants.

Such graphs seem to depict rather well a habitat of atmospheric extremes, making large demands upon all available water, and naturally and necessarily resulting in a xerophytic plant association with a very limited undergrowth and an almost entire absence of herbaceous plants and seedlings. Perhaps nowhere could an association be found more entirely dependent upon vegetative reproduction for its maintenance, since almost without exception any increase in vegetation is the result of subterranean branches.

The records for this association, when considered in relation to the character of its vegetation and compared with those of the other associations, is believed to emphasize the fact that, although these data are for the lower stratum of the vegetation only, they are

[2] Bot. Gaz. **52**:193–208. 1911.

for the critical one, especially in forest associations. Within this stratum develop all the seedlings, and upon their death or survival depends the character of the succeeding vegetation. Therefore, if the vegetation of an association so affects the evaporation rate of this stratum that it permits the survival of seedlings of more mesophytic species, it is evident that a more mesophytic association will develop and succession will be accomplished.

Any individuality in the graphs from the pine dune is plainly due to the evergreen character of the association, and is seen in the low rates in May and October, which are always decidedly below those of the succeeding oak dune association, and are often even lower than those of the oak-hickory and beech-maple forests. That this association is very close to the succeeding one may be seen by referring to table I. Here it will be seen that the mean

TABLE I

MEAN WEEKLY EVAPORATION RATES IN CC. FROM A STANDARD ATMOMETER FOR THREE SEASONS UNDER INVESTIGATION

Association	1910	1911	1912	Average	Comparative rates
Cottonwood dune	21.1	24.6	21.3	22.3	319
Pine dune	11.3	10.3	9.7	10.4	149
Oak dune	10.3	11.8	10.9	11.0	157
Oak-hickory forest	....	9.8	7.8	8.8	126
Beech-maple forest	8.1	7.4	5.6	7.0	100
Edaphic prairie	....	12.5	12.5	12.5	179

evaporation rates were during two of the three years slightly less than those of the succeeding association. The same is true for the average of the rates, but if the comparison be made for the 10 weeks of summer, from the last week of June to the first of September, as shown in table II, the comparative rates are reversed, and the pine dune association has a slightly higher average. This is believed to represent the actual condition during the weeks of greatest stress of moisture conditions.

The graphs of the oak-hickory and beech-maple forests seem to be without any special features other than that they depict the moderate conditions of truly mesophytic associations, while those of the edaphic prairie express the condition of an association

abounding in extremes and fluctuations inferior only to those of the pioneer association dominated by the cottonwood. As might be expected, there is a similarity between the evaporation rate of the prairie and that of the open areas of the oak dune (fig 9).

TABLE II

MEAN WEEKLY EVAPORATION RATES IN CC. FROM A STANDARD ATMOMETER DURING THE 10 MIDSUMMER WEEKS OF THE THREE YEARS UNDER INVESTIGATION

Association	1910	1911	1912	Average	Comparative rates
Cottonwood dune	25.0	30.2	20.3	25.2	315
Pine dune	14.1	12.6	10.3	12.3	154
Oak dune	12.1	13.4	10.1	11.9	149
Oak-hickory forest	....	11.6	6.7	9.2	115
Beech-maple forest	10.2	8.5	5.3	8.0	100
Edaphic prairie	....	15.1	12.4	13.7	171

It is interesting to note that comparative evaporation rates for all the associations, with the exception noted in the case of the pine dune, remain substantially the same whether the comparison is based upon the averages for the entire seasons (table I) or for the weeks of misdummer (table II) only. The comparison is perhaps more striking when the data are represented graphically, either for the individual seasons (fig. 14) or when the data for the three years are combined (fig. 15), when, if it be true that water conditions are the most important factors affecting the establishment of different plant associations, there can be no reasonable doubt that the progressive increase of the moisture content of the habitats indicated by the progressive decrease in the evaporation rates causes a corresponding progressive increase in the mesophytism of the plant associations as a whole, a change which we are accustomed to term *succession*.

As recommended in the writer's preliminary report (*loc. cit.*), the beech-maple forest is taken as the unit of comparison, and the evaporation rates in the other associations are expressed in terms of this unit. Thus, the beech-maple forest being represented by 100, the comparative evaporation rates for the midsummer weeks (table II) in the associations which precede it in the succession are respectively 115, 149, 154, and 315, showing a striking and progressive

increase in the humidity of this stratum of the vegetation as the succession advanced from the pioneer cottonwood to the climax beech-maple association.

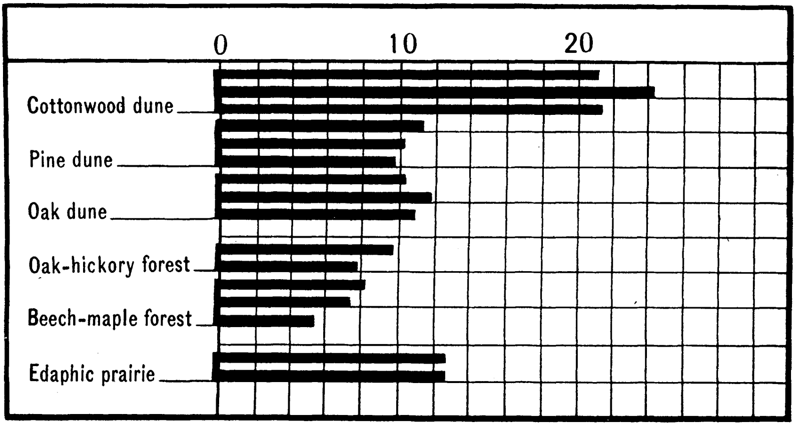

FIG. 14.—Diagram showing the comparative average daily evaporation rates in different associations for the seasons of 1910, 1911, and 1912.

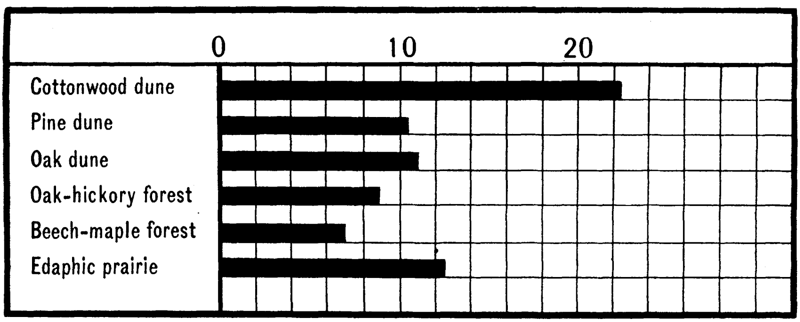

FIG. 15.—Diagram showing the comparative mean average daily evaporation rates in the different associations for the three seasons investigated.

II. Soil moisture

The direct source of the water supply of plants being the moisture in the soil, the amount of this moisture is evidently of the highest importance to vegetation. This has been recognized by many leading ecologists and phytogeographers, but very few data have been made available as to the effects of definite quantitative

amounts upon vegetation, or of the amount and range of the soil moisture in different plant associations. This has been largely due to the difficulty in relating the amount of moisture actually present in the soil to the production of vegetation. It is clear that there can be no direct relation between the percentage of water present in soils and the amount available for plant growth, for a sandy soil with 15 per cent of moisture is at or near saturation, while a stiff clay with 15 per cent of water is so dry that all plants wilt in it, even with a humid atmosphere.

Efforts have been made to establish a standard by which the actual water content of soils could be related to plant production. CLEMENTS (14) determined the amount of water remaining in soils when pronounced wilting occurred, and regarding this as non-available termed it the *echard*, while the difference between the amount actually present in the soil and the echard was the available water, or *chresard*. LIVINGSTON (15) recognized that the water-holding capacity of soils varied and had a fairly constant relation to the soil moisture conditions. Then BRIGGS and MCLANE (16) determined the *moisture equivalent* of soils by the application of a centrifugal force of 1000 times that of gravity, providing a method of measuring and comparing the retentiveness of different soils for moisture acted upon by a definite force. This had the advantage of being measured in absolute terms and of being reproducible within narrow limits of error. It remained for BRIGGS and SHANTZ (17) to refine the methods of determining the percentage of water in soils when permanent wilting occurs in such a plant as the standard Kubanka wheat, giving the *wilting coefficient*, and further to show that a constant relation exists between the moisture equivalent and the wilting coefficient; that is, $\frac{\text{moisture equivalent}}{1.84}=$ wilting coefficient.

They also clearly demonstrated the fact that plants continue to take water from the soil long after the wilting coefficient is reached. The writer, believing that none of the water absorbed from soil whose moisture content is below the wilting coefficient is used for the growth of the organism, has used *growth-water* (18) for the soil moisture in excess of the wilting coefficient.

That the water content of the soil at the time of wilting, or, in other words, the magnitude of the wilting coefficient, is affected by excessive evaporation rates, causing very high transpiration rates, has been shown by BROWN (19) and by CALDWELL (20), although their work also goes to show that it holds perfectly within certain limits differing but slightly from those obtaining in ordinary mesophytic or semi-mesophytic habitats. Although the validity of these objections to the wilting coefficient in extreme conditions is recognized, it is nevertheless believed that it is, especially when determined by the indirect method of BRIGGS and SHANTZ, an efficient means of relating the range of soil moisture to the production of vegetation and an important addition to the equipment of ecological and agricultural investigators.

METHODS

The soil moisture determinations here reported were made in the plant associations described in the previous part of this paper during the years 1911–1912, and for the same months as the atmometer records. In making the determinations, weekly samples, each consisting of 200 to 250 grams of soil, were taken in each of the associations at depths of 7.5 cm. and 25 cm. In order to provide against unnecessary error, each sample consisted of two portions of some 100 grams each, taken from spots several meters apart, care also being taken that no soil was taken nearer than a meter to holes where previous samples had been dug. The soil was placed in wide-mouthed jars, tightly sealed, brought to the laboratory, weighed and dried at a temperature of 100° to 104° C. until it reached a constant weight (about 5–7 days). The percentage of water to the dry weight of the soil was then calculated.

The wilting coefficients of the same soils were determined by both the direct and the indirect methods of BRIGGS and SHANTZ (17). The results from the two methods agreed within the limits of experimental error, which appeared to be much greater in the direct method. This was particularly noticeable in the sandy soil of the dunes, where the wilting coefficient approximates 1 per cent. All the wilting coefficients are the averages of at least 10 determinations.

Those of the clay soils made by the centrifuge, using the formula

$$\frac{\text{moisture equivalent}}{1.84} = \text{wilting coefficient},$$

the moisture equivalent being the amount of water which the soil retains against a centrifugal force of 1000 times gravity, showed very constant results.

The results are represented graphically, the wilting coefficients being represented by broken lines and the range of soil moisture in percentages of the dry weight of the soil by graphs with the weekly intervals as abscissas; while the ordinates represent the percentage of soil moisture present at the weekly determinations. Throughout the diagrams the vertical scale is denoted by figures at the left; and heavy lines are used for the determinations at 7.5 cm., and light lines for 25 cm. depth. The intervals between the graphs and the line denoting the wilting coefficient give the amount of the growth-water.

RANGE IN THE DIFFERENT ASSOCIATIONS

An examination of the accompanying diagrams will show at a glance some of the peculiarities of the water supply of the various associations. The results for the cottonwood dune association for 1911 have already been published (**18**), and show rather surprising results (fig. 16). The water content is rather constant, but seldom more than 5 per cent, a decidedly small amount. However, the wilting coefficient was here found to be less than 1 per cent, the average for many determinations by the indirect method being 0.8 per cent at both depths, the absence of humus and the instability of the soil accounting for the same coefficient at both depths. Considered in relation to this wilting coefficient, the soil moisture is seen to be continually at least twice the amount of water necessary for the growth of such a plant as wheat. This is in striking contrast to the desert-like aspect of this association, due to the almost complete absence of herbaceous undergrowth. Doubtless this constancy in soil moisture is largely due to the conserving action of a dry mulch of 3 to 5 cm. thickness maintained by the action of the wind upon the sand and to the small quantities withdrawn by the sparse vegetation. The record for 1912 (fig. 17) differs in no

important particular from that of the previous year, an unfailing supply of growth-water being maintained, although its average amount during the weeks of midsummer is slightly less.

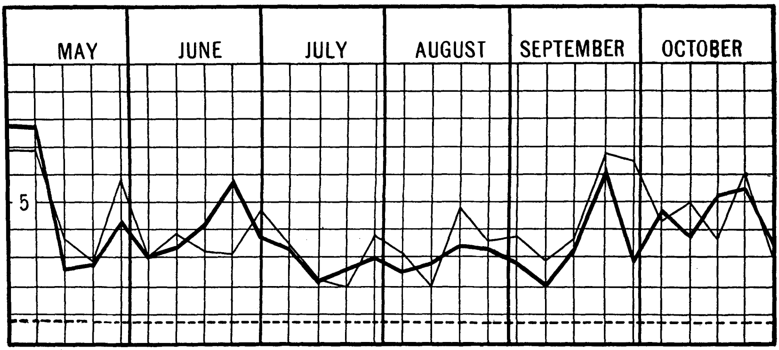

FIG. 16.—Graphs showing the range of soil moisture in the cottonwood dune for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by a broken line.

In the next association, the pine dune, the accumulation of humus increases the wilting coefficient to 1.1 per cent at 7.5 cm.,

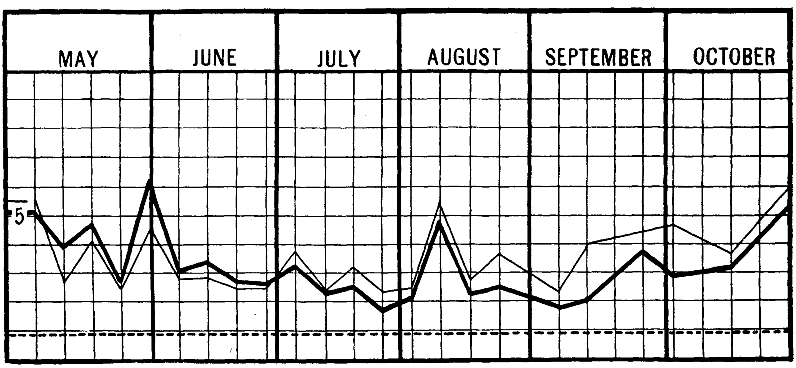

FIG. 17.—Graphs showing the range of soil moisture in the cottonwood dune for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by a broken line.

and to 1.0 per cent at 25 cm. The range of the moisture throughout both 1911 (fig. 18) and 1912 (fig. 19) is more irregular than in the previous association, especially in the upper stratum, and what

is more important, during three different weeks of each year the supply falls almost to or actually below the wilting coefficient. It is thus an association in which the growth-water fails repeatedly, and consequently with respect to its water supply is decidedly more

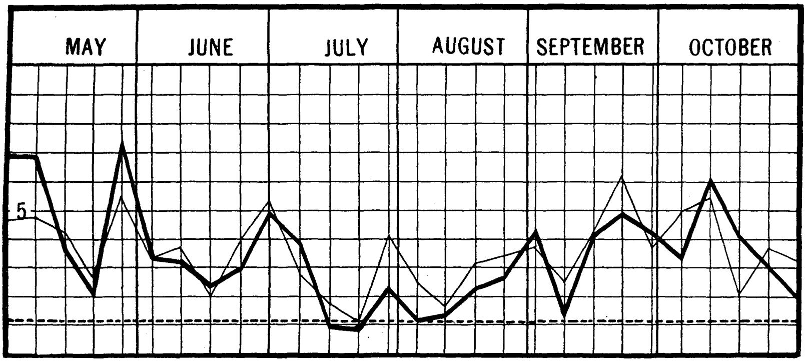

FIG. 18.—Graphs showing the range of soil moisture in the pine dune for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by broken lines.

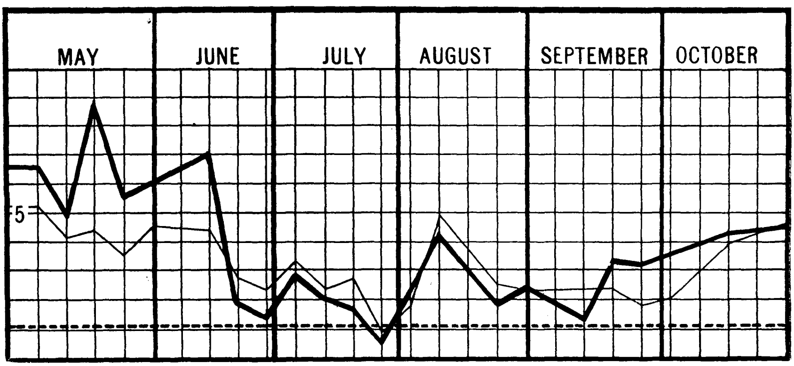

FIG. 19.—Graphs showing the range of soil moisture in the pine dune for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by broken lines.

xerophytic than the cottonwood dune. Reasons for the failure of the water supply may be found in the comparative absence of the conserving mulch of dry non-conducting soil, and in the much larger demands made by the denser stand of vegetation. The plentiful

supply during the weeks of spring permits the growth of a mesophytic herbaceous spring flora.

The open character of the forest on the oak dunes has brought no increase of humus, as indicated by wilting coefficients of 1.1 per

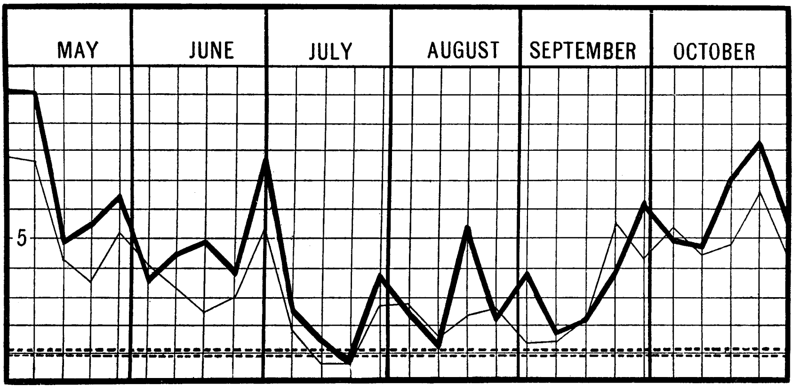

FIG. 20.—Graphs showing the range of soil moisture in the oak dune for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

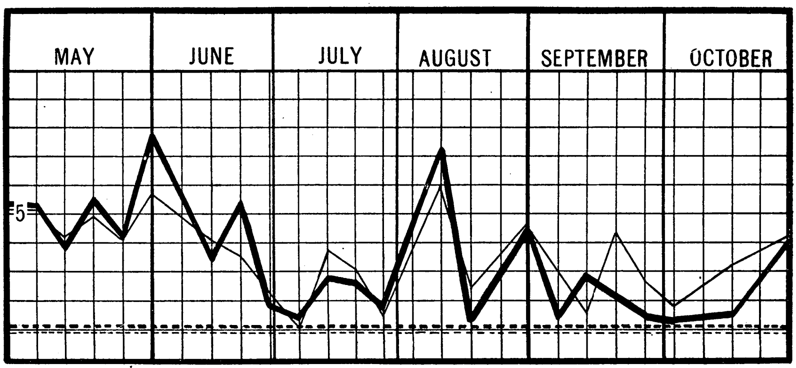

FIG. 21.—Graphs showing the range of soil moisture in the oak dune for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

cent and 0.9 per cent respectively for the 7.5 cm. and 25 cm. strata. The seasonal range of soil moisture is irregular (figs. 20, 21), and several times each season it approximates or falls below the wilting coefficients. The graphs indicate comparatively xerophytic

soil conditions approximately similar to those of the preceding association.

The results for the oak-hickory forest for 1911 have already been published (**10**), but are reproduced here for the sake of completeness, especially since the record for 1912, owing to a series of interruptions and accidents, is too fragmentary to be of any value. The soil here is a clay with an admixture of gravel, and differs in a striking manner from the sand in its moisture-holding capacity, shown by wilting coefficients of 9 per cent and 9.5 per cent at

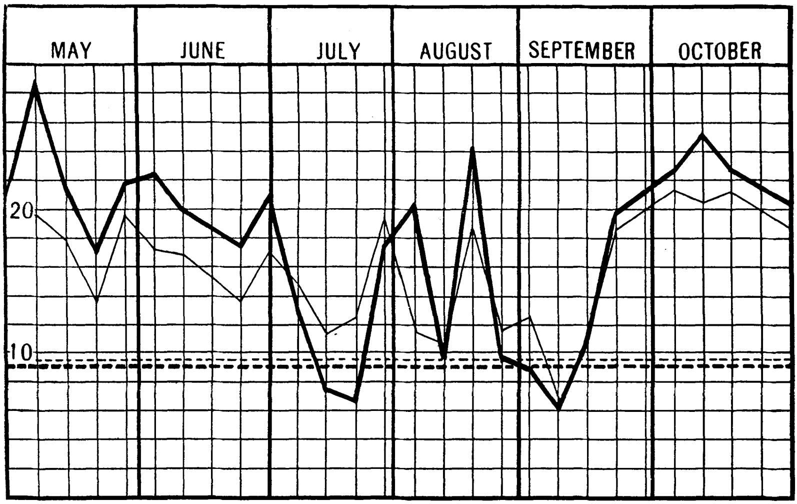

FIG. 22.—Graphs showing the range of soil moisture in the oak-hickory forest for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

depths of 7.5 cm. and 25 cm. The fluctuations in the soil moisture are great, particularly at 7.5 cm. (fig. 22). Although the water content of the soil at 35 cm. once falls below the wilting coefficient, the average amount of growth-water for the midsummer weeks is considerable (table III), much greater in fact than in any preceding association, indicating decidedly more mesophytic soil conditions.

It may be noted that the wilting coefficients now given for this and the succeeding association differ slightly from those formerly published. This is due to their redetermination by more careful methods, particularly to the use of the indirect method.

The ravine of the oak-hickory forest, with its abundance of humus, gave wilting coefficients of 16.3 per cent and 12.2 per cent

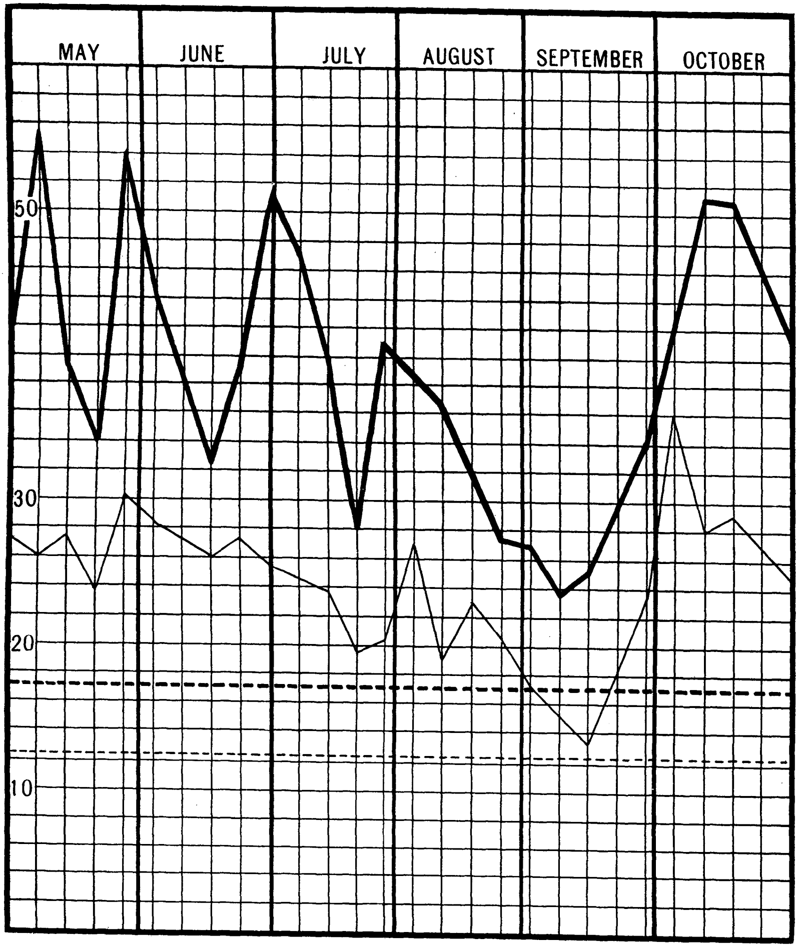

FIG. 23.—Graphs showing the range of soil moisture in the ravine of the oak-hickory forest for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by broken lines.

respectively for the soil at depths of 7.5 cm. and 25 cm. The graphs (fig. 23) show the presence of a constant and abundant supply of growth-water throughout the season. This would quite agree with

the hyper-mesophytism of rich floodplains, of which this may be regarded as a type.

The climax beech-maple forest shows the accumulation of humus in its wilting coefficient of 9.5 per cent at 25 cm., being increased to 13.5 per cent at 7.5 cm. In this association the soil moisture determinations were made only every second week, but the graphs (figs. 24, 25) show a constant and generous supply of

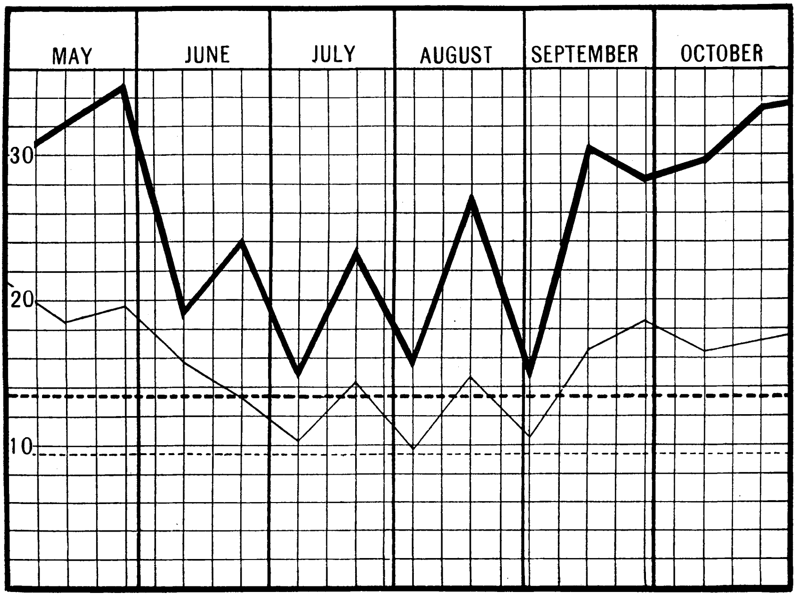

FIG. 24.—Graphs showing the range of soil moisture in the beech-maple forest for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

growth-water, indicative of truly mesophytic conditions. The supply of growth-water is unfailing. As in the other associations, the upper stratum shows the larger amount of variation. A comparison of the two seasons will show that, while the averages are about the same, the year 1912 shows a much greater uniformity in the range of the moisture supply.

The results for the prairie association are more difficult to interpret. The range plotted in fig. 26 is the mean of the two stations

reported by HARVEY (13) for the season of 1911, while fig. 27 gives the results obtained by Miss NEWLON in 1912. The wilting coefficients of 24 per cent at 7.5 cm. and 21 per cent at 25 cm. indicate soil with a high water-retaining capacity. This soil is at or near saturation point early in the spring, just as the growing season begins (figs. 26, 27); in fact it seems probable that the amount of water present is not only in excess of all requirements of the

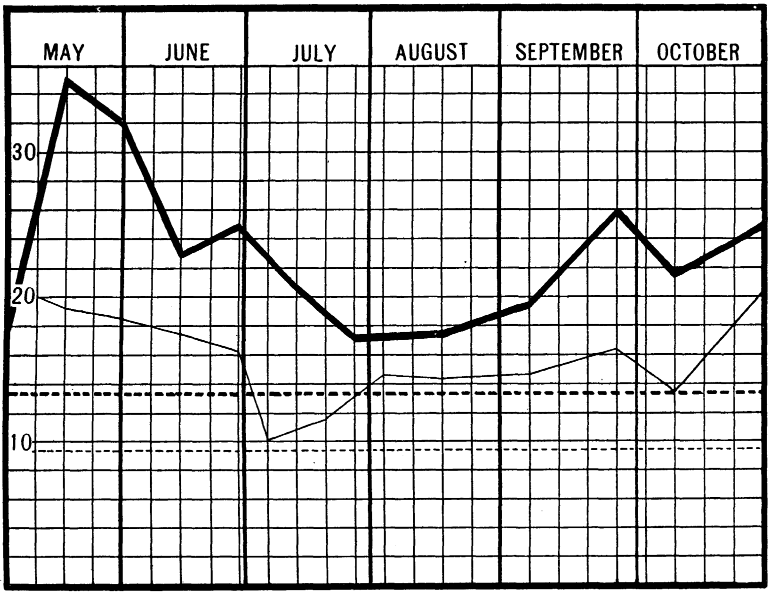

FIG. 25.—Graphs showing the range of soil moisture in the beech-maple forest for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

vegetation, but even in such abundance as to prove detrimental to many plants. Late in the fall the supply is also very large. In striking contrast is the small and irregular supply during midsummer, when the wilting coefficient is more than once reached or approximated. In general the habitat is shown to be one of extreme fluctuations in respect to its moisture supply, conditions which may help to account for the absence of trees. It is particularly xerophytic during late summer.

GENERAL CONCLUSIONS

An examination of all the graphs showing the range of soil moisture, as well as a general consideration of the conditions of growth

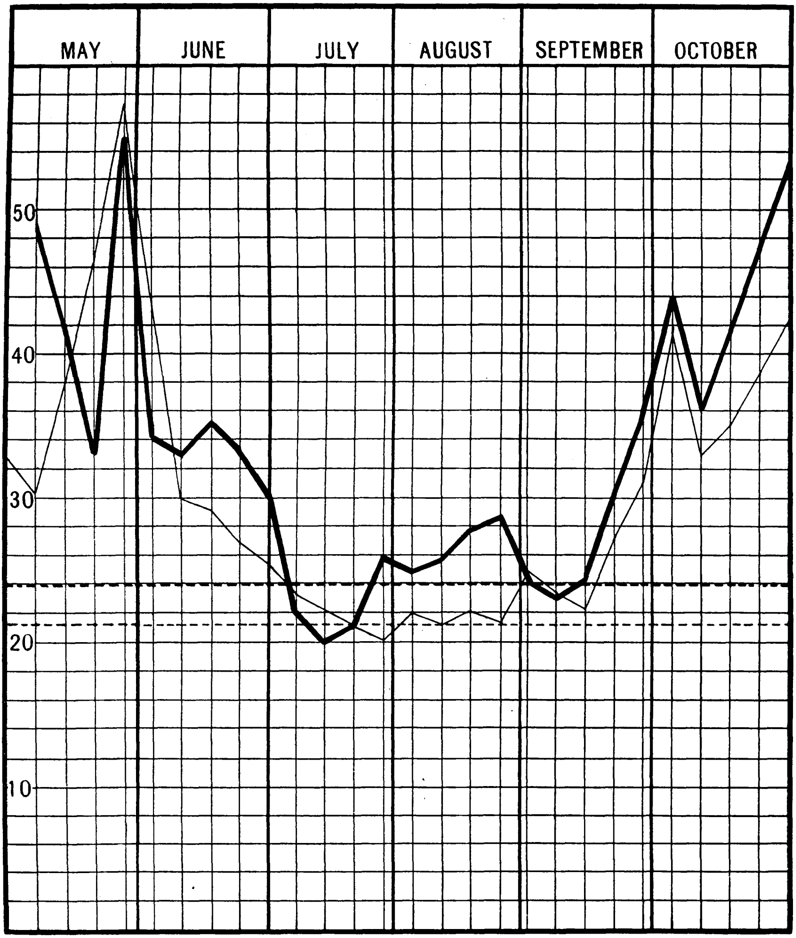

FIG. 26.—Graphs showing the average range of the soil moisture in the edaphic prairie for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines (after HARVEY).

in these associations, indicates that only during midsummer is there any scarcity in the supply in any of the habitats. It has seemed desirable, therefore, and even more necessary than in the evapora-

tion studies, to limit our comparisons to this period of stress, and to establish the rather arbitrary limit of the 10 weeks from the last of June to the first of September. A summary for these weeks appears in table III.

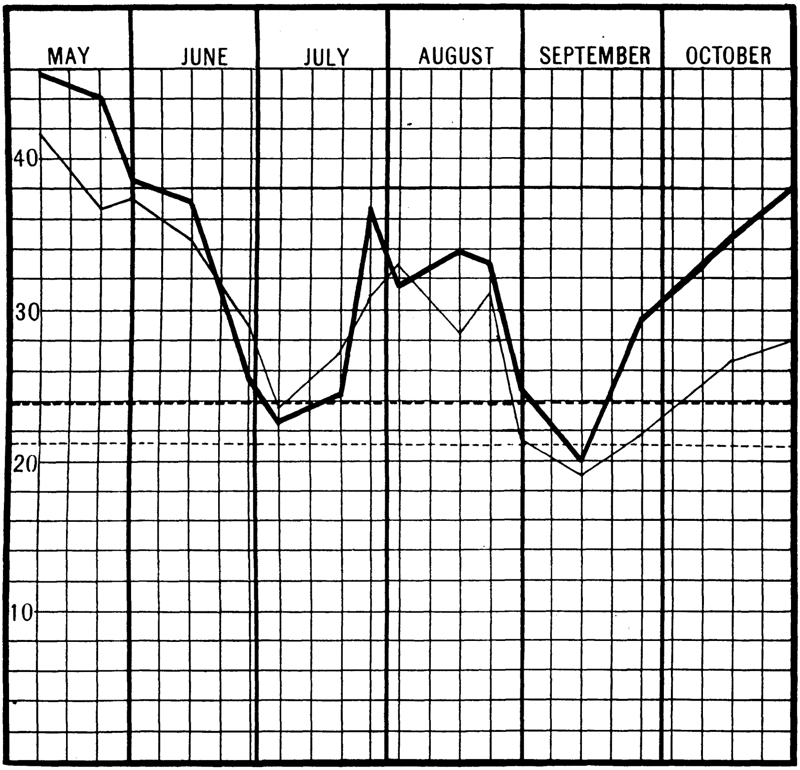

FIG. 27.—Graphs showing the range of soil moisture in the edaphic prairie for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

No one can realize more fully than does the writer the limitations of the data or the desirability of having them supplemented by more numerous determinations, especially from deeper strata. These limitations will make the conclusions more or less provisional and subject to modification and correction in the future. The most interesting and profitable comparisons are doubtless those to be made from a consideration of the growth-water data shown

in table III, and especially as expressed in the sixth and seventh columns, which contain the mean percentages of growth-water and the comparative amounts, the beech-maple forest being taken as a standard and its mean growth-water represented by 100. In the five associations that form the succession, the mean growth-water for midsummer of the two seasons will be found, if we except the cottonwood dune, to form a progressive series, the most mesophytic association having the largest amount. This was exactly what was supposed to be the situation, but hitherto no quantitative data of such moisture relationships have been available, and it has been

TABLE III

WILTING COEFFICIENTS AND MEAN PERCENTAGES OF GROWTH-WATER IN THE VARIOUS ASSOCIATIONS DURING THE 10 MIDSUMMER WEEKS OF 1911–1912

Association	Depth in cm.	Wilting coefficient	Growth-water				Ratio between evaporation and growth-water
			1911	1912	Mean	Comparative am'ts	
			per cent	per cent	per cent	per cent	
Cottonwood dune..	7.5 25.0	0.80 0.80	2.2 2.6	1.8 2.0	2.15	49	11.7
Pine dune........	7.5 25.0	1.10 1.00	0.9 1.7	0.7 1.3	1.15	26	10.7
Oak dune........	7.5 25.0	1.10 0.90	1.4 0.8	1.4 1.5	1.27	29	9.37
Oak-hickory......	7.5 25.0	9.0 9.5	3.2 3.3	....	3.3	75	2.78
Beech-maple......	7.5 25.0	13.5 9.5	5.5 3.0	5.0 4.0	4.4	100	1.81
Prairie...........	7.5 25.0	24.0 21.0	4.0 4.9	4.0 5.9	4.7	107	2.91

impossible to tell how much an association differs in its water conditions from the preceding or succeeding association. As has already been stated, the cottonwood dune, with a larger and more constant water supply than the two succeeding associations, must owe its surplus to the conserving power of its dust mulch and to the small outgo due to the paucity of its vegetation.

The comparative amounts of growth-water indicate even more clearly the relationship existing between the available water supply of the associations, and should serve to emphasize the fact that the progressive increase in the water-retaining power of the

soil, due largely to its increased humus content, must play no inconsiderable rôle in causing the succession here culminating in the mesophytic beech-maple forest. Little need be said concerning the rank of the prairie, in respect to its soil moisture in comparison with the other associations under consideration, further than to point out that its soil has a very great water capacity, and that over against its large amount of growth-water should be placed the fact that the supply completely fails at intervals. More investigation must be made before more definite comparisons can be made.

Another and still more important comparison may be instituted among the associations under investigation by considering the ratio between the average mean weekly evaporation rates for the 10 midsummer weeks of the years 1910–1912 and the mean growth-water for the same period. These ratios are expressed in the final column of table III. In determining these ratios it is recognized that the units of measurement in the case of the evaporation rates and the soil moisture are not directly comparable. Still it is thought that the comparison is a legitimate one, and institutes a quantitative summation of the mesophytism of the habitats which is valuable and exceeds in accuracy anything hitherto attained. It is true that these habitats are limited to the lower stratum of the aerial and the upper strata of the subterranean vegetation, but, as previously pointed out, these are the portions of the habitat that are of critical importance in the establishment and maintenance of the associations, because in them the seedlings, both woody and herbaceous, develop. An extension of the habitats by the addition of the higher strata of the air and the lower strata of the soil containing all the aerial and subterranean portions of the vegetation would doubtless modify and perhaps decrease the steepness of the gradient between the various ratios. The ratios may either be compared directly, remembering that the mesophytism of the various habitats varies in inverse ratio with the numbers expressing these ratios, or the beech-maple forest may again be taken as the standard and represented by 100, when the direct ratio of the mesophytism of the corresponding portions of the oak-hickory forest, the oak dune, the pine dune, and the cottonwood dune will be respectively 65, 20, 17, and 15. The prairie expressed in similar terms will be 62. These

comparative values of the moisture factors show such a surprising rate of increase as one proceeds from the pioneer to the climax associations that it cannot be doubted that such a change in water conditions must be one of the chief factors, if not the most important cause, of the succession of associations from the more xerophytic to the more mesophytic.

Summary

1. These data represent the evaporation rates in the lower aerial stratum and the range of soil moisture in the upper subterranean strata of the vegetation of the various associations, but these must be regarded as critical regions, since within them develop the seedlings which determine the character of succeeding vegetation.

2. Evaporation at different stations in the same plant association exhibits variations similar in character and degree.

3. The rate of evaporation in the cottonwood dune association, both by its great amount and by its excessive variation, seems a quite sufficient cause for the xerophytic character of the vegetation and for the absence of undergrowth, in spite of the constant presence of growth-water.

4. The pine and oak dune associations resemble one another closely both in their mean evaporation rates and in their supply of growth-water. The former is slightly more xerophytic during the midsummer weeks.

5. The vernal vegetation of the pine dune is quite as mesophytic as that of the succeeding association, thus agreeing with its lower evaporation rate during that portion of the year.

6. The evaporation rates and the amount of growth-water in the various associations vary directly with the order of their occurrence in the succession, the pioneer being the most xerophytic in both respects.

7. The ratios between evaporation and growth-water in the beech-maple forest, oak-hickory forest, oak dune, pine dune, and cottonwood dune associations have been shown to have comparative values of 100, 65, 20, 17, and 15 respectively, and the differences thus indicated are sufficient to be efficient factors in causing suc-

cession. The corresponding value of this ratio in the prairie association is 62.

8. The midsummer conditions of the prairie association seem to be decidedly xerophytic.

Grateful acknowledgment is made of the cooperation and advice given by Professor HENRY C. COWLES, under whose direction the investigation has been conducted, and of the assistance of Messrs. WADE McNUTT, E. M. HARVEY, C. SHIRK, and Miss L. NEWLON in collecting data.

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LITERATURE CITED

1. LIVINGSTON, B. E., Evaporation and plant habitats. Plant World **11**:1–10. 1908. Also see: LIVINGSTON, GRACE J., An annotated bibliography of evaporation. Monthly Weather Review **36–37**:1908–1909.
2. COWLES, H. C., The ecological relations of the vegetation of the sand dunes of Lake Michigan. BOT. GAZ. **17**:117, 169–202, 281–308, 361–391. 1899.
3. TRANSEAU, E. N., A simple vaporimeter. BOT. GAZ. **49**:459–460. 1910.
4. NICHOLS, G. E., A simple revolving table for standardizing porous cup atmometers. BOT. GAZ. **55**:249–251. 1913.
5. LIVINGSTON, B. E., Operation of the porous-cup atmometer. Plant World **13**:111–119. 1910.
6. BROWN, W. H., Evaporation and plant habitats in Jamaica. Plant World **13**:268–272. 1910.
7. FULLER, G, D., Germination and growth of the cottonwood upon the sand dunes of Lake Michigan near Chicago. Trans. Ill. Acad. Sci. **5**:137–143. 1912.
8. GLEASON, H. A., and GATES, F. C., A comparison of the rates of evaporation in certain associations in central Illinois. BOT. GAZ. **53**:478–491. 1912.
9. COWLES, H. C., The physiographic ecology of Chicago and vicinity. BOT. GAZ. **31**:73–108, 145–182. 1901.
10. McNUTT, W., and FULLER, G. D., The range of evaporation and soil moisture in the oak-hickory forest association of Illinois. Trans. Ill. Acad. Sci. **5**:127–137. 1912.
11. FULLER, G. D., Evaporation and the stratification of vegetation. BOT. Gaz. **54**:424–426. 1912.
12. TRANSEAU, E. N., The relation of plant societies to evaporation. BOT. GAZ. **45**:217–231. 1908.
13. HARVEY, E. M., Evaporation and soil moisture on the prairies of Illinois. Trans. Ill. Acad. Sci. **6**:92–99. 1913.

14. CLEMENTS, F. E., Research methods in ecology. pp. 334. 1905.
15. LIVINGSTON, B. E., The relation of desert plants to soil moisture and to evaporation. Carnegie Institution of Washington, Publ. no. 50. pp. 78. 1906.
16. BRIGGS, L. J., and MCLANE, J. W., The moisture equivalents of soils. U.S. Dept. Agric., Bur. of Soils, Bull. 45. 1907.
17. BRIGGS, L. J., and SHANTZ, H. L., The wilting coefficient for different plants and its indirect determination. U.S. Dept. Agric., Bur. Plant Ind., Bull. 230. 1912; BOT. GAZ. **51**:210–219. 1911; and **53**:20–37, 229–235. 1912.
18. FULLER, G. D., Soil moisture in the cottonwood dune association of Lake Michigan. BOT. GAZ. **53**:512–514. 1912.
19. BROWN, W. H., The relation of evaporation to the water content of the soil at the time of wilting. Plant World **15**:121–134. 1912.
20. CALDWELL, J. S., The relation of environmental conditions to the phenomenon of permanent wilting in plants. Physiological Researches **1**:1–56. 1913.